Acta Zool. Fennica 196:101–106
Helsinki 28 February 1995
ISBN 951-9481-41-9
ISSN 0001-7299
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XI International Colloquium on Soil Zoology, Jyväskylä, Finland, 10–14 August, 1992

Interspecific interactions in the soil community[1]

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One goal of soil biology is the understanding of the trophic structure of the biota in the soil-litter system: species populations are aggregated to trophic elements and subsystems as constituents of the whole system. A key question is how trophic populations are limited. It is suggested that a pragmatic methodological tool for studying the trophic structure of the soil is the delimitation of "interacting biotic system elements", which communicate with other elements via interfaces. In a bottom-up approach the whole system is assembled using these biotic elements. This concept is exemplified for the soil community of a temperate forest on mull soil with emphasis on Lumbricidae, Collembola and Chilopoda. There are indications that lumbricids and chilopods tend to be limited by resource availability (donor-control) whereas Collembola endure high predation pressure (tendency for predator control).

1. Introduction

The soil is inhabited by a high number of microfloral and animal populations which are connected by an intricate complex of trophic, competitive and/or mutualistic interrelations and subjected to the influence of abiotic environmental factors. Variability and stochasticity in the system tend to obscure general patterns.

There are several possible approaches in analysing interspecific interactions in the soil community:

1) The natural history approach emphasizing the biological diversity of soil organisms (Elton 1966, Wallwork 1976, Tischler 1984, Schaefer 1991a).
2) The "soil science" approach distinguishing delimitable microhabitats with the associated microflora and fauna (e.g. the rhizosphere) (Richards 1987, Anderson 1988, Paul & Clark 1989).
3) The "typological" approach analysing types of interaction, starting with mutualism and ending up with interspecific competition and predation. Such is the approach of textbooks on ecology (e.g. Begon et al. 1990).
4) The functional approach studying the effects of biotic interactions on system processes such as chemical flux or decomposition (e.g. Fitter 1985, Edwards et al. 1988, Anderson 1988, Verhoef & Brussaard 1990, Wolters 1991a).
5) The theoretical approach with the application of food web theory to the community of soil organisms (Schoener 1989, Lawton 1989, Pimm et al. 1991) or the introduction of other theoretical concepts such as the dualism of community-oriented and process-oriented approach or hierarchy theory (O'Neill et al. 1986).

One challenge in this respect is the analysis of the trophic structure of the whole soil community. It should be generally accepted that the species with its particular manifestations of life is the basic biological unit of any study in the field of soil biology. How can this species-specific approach lead to an analysis of the whole system? This paper outlines a possible methodology which could be used in such studies.

2. A conceptual model of the soil–litter community

A conceptual model of the trophic structure of the soil–litter community has to take into account the high biotic diversity and the high degree of spatial and temporal compartmentalization on different scales. The interactions between populations are numerous and manifold. Organisms are concentrated in a thin zone in the ecosystem (litter and the upper centimeters of the soil) where they are intimately associated with the organic and inorganic matrix. The system is dependent on litter input. The dominant system processes

[1] The paper is dedicated to Prof. Dr. Wolfgang Tischler, University of Kiel, on the occasion of his 80th birthday.

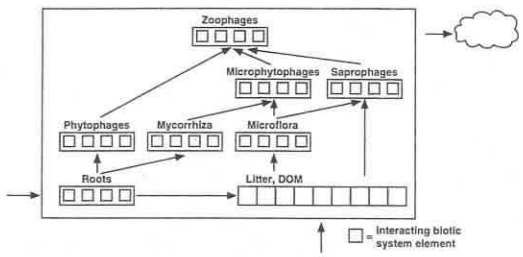

Fig. 1. A conceptual model of the trophic structure of the soil-litter system. Arrows denote the flow of carbon via the food chain. Mutualistic and competitive relationships are not indicated. DOM = dead organic matter.

are the decomposition of organic material and the mineralization of important bioelements (Swift et al. 1979, Schaefer 1989). The diversity of system components, the diversity of linkages between elements and the complex interactions between them constitute an intractable problem in studying the soil community.

A first step in structuring the system for trophic analysis is the aggregation of soil animal and microfloral populations to functional groups and subsystems in relation to their food resources (Swift et al. 1979, Petersen & Luxton 1982, Verhoef & Brussaard 1990, Schaefer 1990). Main trophic elements among the animals are phytophages, microphytophages, saprophages and zoophages (Fig. 1); further subdivisions are helpful, such as micromycophages and bacteriophages among microphytophages or macrosaprophages and microsaprophages among saprophages. However, such functional classifications are imperfect copies of the natural situation and hence often criticized. Faber (1991), for instance, introduces the concept of leagues, spatially stratified trophic groups with different functions in the community.

In a second phase of analysis a whole-system model is assembled (cf. Fig. 1). This is a crucial and difficult process, because it is a reductionist approach focussing on essential elements of the system: key groups and key functions. Within one trophic category several biotic units with different functions usually have to be differentiated (named "interacting biotic system elements" in Fig. 1). The result is a model of the trophic structure of the system. If in the decomposition system the predators are united on one trophic level, the web comprises two levels for the pathway of food via the saprophages and three levels for the pathway via microflora and microphytophages. Interactions (denoted by arrows in the models) can be based upon simple feeding relations ("connectedness web"), flow rates ("energy flow web") or functionally important interrelations ("functional web") (Hunt et al. 1987, Wolters 1991a). Food webs tend to overemphasize negative interactions (predation, competition) and to underestimate mutualistic relationships (Wolters 1991a). Within the decomposition subsystem the biota have many indirect effects on the abiotic and biotic soil environment (for instance via bioturbation) and control element flux (mineralization). Nutrient uptake by plant roots and plant growth serve as integrating filters: higher-order, functional measurements of the net products of the activities of soil biota (Anderson 1988, Setälä & Huhta 1991, Wolters & Stickan 1991).

3. The study of soil animal communities: patterns and hypotheses

Although a high degree of stochastic variation occurs, some general patterns in the trophic organization of soil animal communities can be observed (Swift et al. 1979, Petersen & Luxton 1982, Anderson 1988, Schaefer 1991c): high species diversity within trophic groups; tendency to trophic generalism; feeding loops; short food chains (cf. Fig. 1); relatively constant biomass of saprophages; fluctuating mesofaunal populations; presence of a high number of predators; and continuity in litter decomposition.

Hypotheses can be formulated to explain the observed patterns. For instance, faunal diversity may be due to the spatial heterogeneity of the soil-litter system and the diversity of utilisable food resources (Anderson 1975, Schaefer 1991a). The stability in structure and function can be related to compensatory activities of the populations and the dampening effects of filters in the hierarchical organisation of the system (Wolters 1991a). There is reason to believe that some of the patterns cannot be explained satisfactorily, because the corresponding hypotheses cannot be falsified (Peters 1990). It is important to have concrete, realistic concepts and questions, which can be moulded into testable hypotheses. One set of such hypotheses concerns a basic question about community interaction in soil: the limitation of populations by resource availability (donor control) or by enemies (predator control). In the first instance the organisation of the soil animal community is more based on competition, in the second instance on predation.

In this connection three possible sets of hypotheses can be proposed:

1) Bottom-up limitation: The decomposers as a whole are food-limited. The saprophagous macrofauna tends to be limited by its food resources. Certainly only part of the decomposers is donor-controlled. For other populations predators or competitors are limiting factors. Microphytophages are partly donor- and partly predator-controlled. Predators are limited by their food resources.
2) Top-down limitation: Microphytophages and saprophages are limited to a large extent by predation. In order to explain continuous and more or less constant decomposition, it must be assumed that microfloral populations compete for food resources or that microflora and some saprophages invade spaces in the resource matrix that are competitor-free due to effects of the predators.
3) Limitation by a mixture of biotic and abiotic factors without an overall pattern on the community level. This means, for instance, that individual decomposer populations are determined to a large extent by stochastic processes, by the spatio-temporal variation in resource availability and by resource quality.

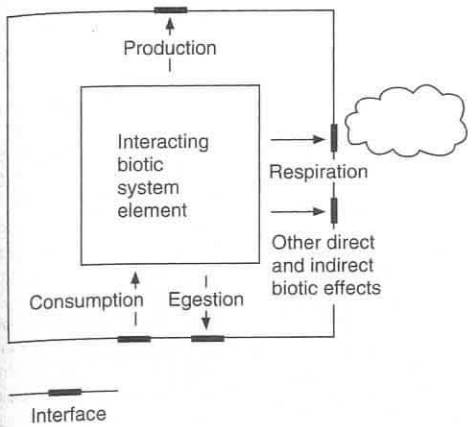

Fig. 2. The interacting biotic system element. Interfaces with other system elements are indicated by a thick bar. Straight arrows denote carbon flow. Wavy arrow indicates direct and indirect interrelations with other soil biota.

For lack of space I do not attempt to discuss the background behind current theories about the trophic organization of animal communities (c.f. Hairston et al. 1960, Slobodkin et al. 1967, Menge & Sutherland 1976, Sih et al. 1985, Lawton 1989). Control by food in the two-level chain of saprophages and predators, and an alternating control by predation and competition in the three-level chain of microflora (dominant interaction, competition), microphytophages (dominant interaction, predation) and predators (dominant interaction, competition) would support arguments presented by Hairston et al. (1960) ("HSS hypothesis").

The hypotheses can be tested experimentally. An experimental increase (or decrease) of litter and DOM (of the quality required by the populations) should lead to an increase (decrease) of animal decomposer biomass if hypothesis (1) applies, should cause no change in animal decomposer biomass if (2) is right, or should have no predictable outcome if (3) applies.

An experimental addition (exclusion) of predators should have no significant effect on animal decomposers if (l) applies, should cause a decrease (increase) of animal decomposer biomass if (2) is correct, or should induce no predictable effects if hypothesis (3) is right.

4. A methodological tool: the analysis of interacting biotic system elements

An "interacting biotic system element" (Fig. 2) may serve as a link between the descriptive or experimental analysis of the soil community on the one hand and conceptual ideas about its organisation on the other hand. The unit can be regarded as a trophic guild comprising functionally similar populations (e.g. the populations of all endogeic earthworms of a habitat). The interacting biotic element has definable interfaces to its biotic environment.

Steps to differentiate the populations of the soil community into such units are: the systematic acquisition of knowledge about biology and ecology of the populations in the soil; aggregation of recognizably similar (in many cases taxonomically related) populations to biotic (organismic) units; quantification of the energy or carbon budget of this unit; evaluation of indirect effects of this unit on other biota by field and laboratory experiments; connections of the interacting biotic element at interfaces to its biotic surroundings.

Patterns and processes in the resulting interaction web can yield hypothetical information about the organization of the soil community. Field experiments at the ecosystem level (i.e. addition or exclusion of populations) serve to test these hypotheses.

5. The community of a European mull beech forest soil as an example

The soil and litter fauna of a beech forest on mull soil ("Göttinger Wald") near Göttingen (Germany) has been studied in detail for more than 10 years (Schaefer 1989, 1990, 1991b, 1991c, Schaefer & Schauermann 1990) and hence is suitable for exemplifying the proposed line of trophic system analysis.

5.1. The food web

For the sake of simplicity, trophic elements of the forest are based upon taxonomic units. In many cases a single taxonomic unit has had to be subdivided into different trophic categories, often at the level of the individual species. The species-rich fauna is characterized by high trophic diversity. Main trophic relations as a result of the long-term studies in the forest are depicted in Fig. 3. The food web of the decomposition system is complex even in this rather simplified structure. Some dominant animal populations — mainly the macroconsumers — are persistent in time with a rather constant biomass. On the contrary, the abundance and biomass of mesofaunal groups fluctuate from year to year.

5.2. Three complexes of interacting biotic elements

Three complexes of interacting biotic elements from different positions in the web are analysed in more detail: earthworms (Lumbricidae) as "saprophages", springtails (Collembola) as "microphytophages" and centipedes (Chilopoda) as "zoophages" (predators).

Lumbricidae

Earthworms with a mean biomass of about 10 g dry wt / m^2 constitute two thirds of total faunal biomass (Schaefer 1990). About one half of lumbricid biomass (56%) belongs to the anecic species *Lumbricus terrestris;* the other half (40%)

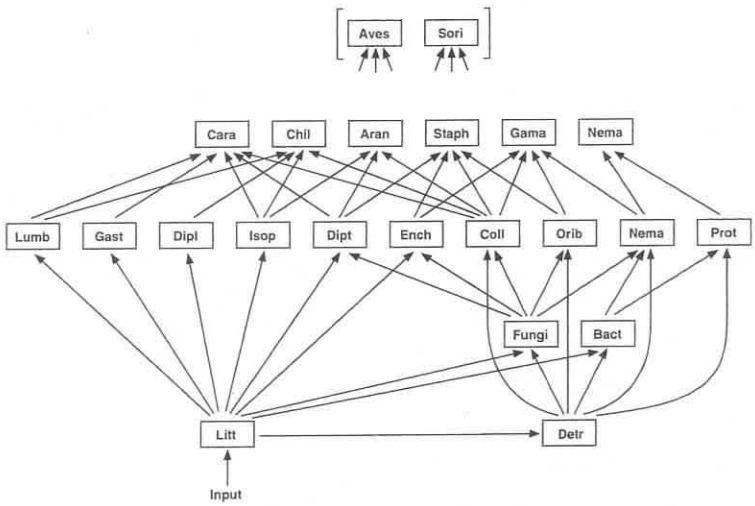

Fig. 3. The food web of a temperate forest with mull soil ("Göttinger Wald", Germany). Only important food relations are indicated. Litt = litter, Detr = detritus, Bact = Bacteria, Lumb = Lumbricidae, Gast = Gastropoda, Dipl = Diplopoda, Isop = Isopoda, Dipt = Diptera, Ench = Enchytraeidae, Coll = Collembola, Orib = Oribatei, Nema = Nematodes, Prot = Protozoa, Cara = Carabidae, Chil = Chilopoda, Aran = Araneida, Staph = Staphylinidae, Gama = Gamasina, Sori = Soricidae.

comprises endogeic species (mainly *Aporrectodea* spp.); the epigeic species are less well represented; they attain 4% of the biomass (Judas et al. 1989). Taking these life-form categories as a basis, three biotic elements can be distinguished: LUMB 1 (with incorporation of litter into the soil), LUMB 2 (with litter feeding) and LUMB 3 (with substrate and detritus feeding) (Fig. 4a). A high amount of litter and detritus is processed. A high proportion of litter is comminuted via egestion. Only a small part of produced carbon is consumed by predators.

There are many other interfaces with the biotic environment of the earthworm populations in the forest. As laboratory experiments demonstrated, lumbricids prefer protozoa-rich soil (Wellner & Bonkowski, unpublished results). Enchytraeids avoid soil populated by earthworms (Schlaghamersky, unpublished results). Earthworms have many indirect effects, for instance, stimulating microfloral activity as demonstrated for nitrogen-mineralizing bacteria (Scheu 1987) and wood-decomposing fungi (Scheu 1993). In laboratory experiments with the forest herb Elymus *europaeus,* the presence of endogeic earthworms influenced above-ground and below-ground plant production (Alphei, Bonkowski & Scheu, unpublished results; Klebsch et al., this volume). Earthworms are controllers of biotic activity in the soil by their large number of indirect effects, which have yet to be studied in detail.

Summing up: the high ingestion rates of lumbricids in the pathway of litter and detritus in comparison to the resource available, the low predation pressure they experience, and their persistence in time with high biomass (Judas et al. 1989), may be regarded as an indication of donor control of these decomposers (hypothesis (1)). In accordance with this evidence, exclusion of earthworm predators did not cause an increase in earthworm biomass (Judas 1989). An experimental exclusion of canopy leaf-litter fall in the field led to a sharp drop in lumbricid biomass; on the other hand, as a disproof of hypothesis (l) an experimental increase of litter input did not result in higher biomass values of earthworms (Judas 1990). This inability of earthworms to utilize the additional food resources may be due to a deterioration of environmental conditions in the soil-litter system with densely packed thick litter strata.

Collembola

The collembolans of the forest constitute about 1% of faunal biomass; their density and biomass fluctuate widely from year to year. About one-half of material they consume is detritus; the other half consists of fungi and algae (elements COLL 1 and COLL 2 of Fig. 4b): Wolters (1985) gives values of 60% and 36% respectively. It is improbable that DOM (detritus) is limiting for Collembola populations, as their role as detritus-processors is minimal. The grazing pressure upon fungal mycelia could only be assessed if production rates of fungal biomass were known. Taking fungal mass as a minimal estimate of production, it appears improbable that the availability of fungal material restricts the development of collembolan populations. However, further experiments are needed to test the quantitative importance of Collembola as fungal feeders and their dependence on certain fungal species as preferred food. Collembolans exert many indirect effects on fungal populations by grazing on the mycelia; in many cases microbial activity is stimulated (Wolters 1991b).

The production of collembolan biomass is low compared with possible feeding pressure by predators such as carabid beetles or chilopods. Because some collembolan populations are prone to predation and live in a superabundance of detritus and fungal mass, it can be argued that they tend to be predator-limited. Field experiments with artificial manipulations of the density of spiders (Stippich, unpublished results) and centipedes (Poser 1990) demonstrated that a high number of litter springtails were consumed by spiders and centipedes. However, convincing documentation of the importance of these predatory populations for limiting collembolan density requires more systematic and realistic experiments. A further key question is the extent to which collembolan populations in the forest are capable of depleting their most preferred fungal food in the field.

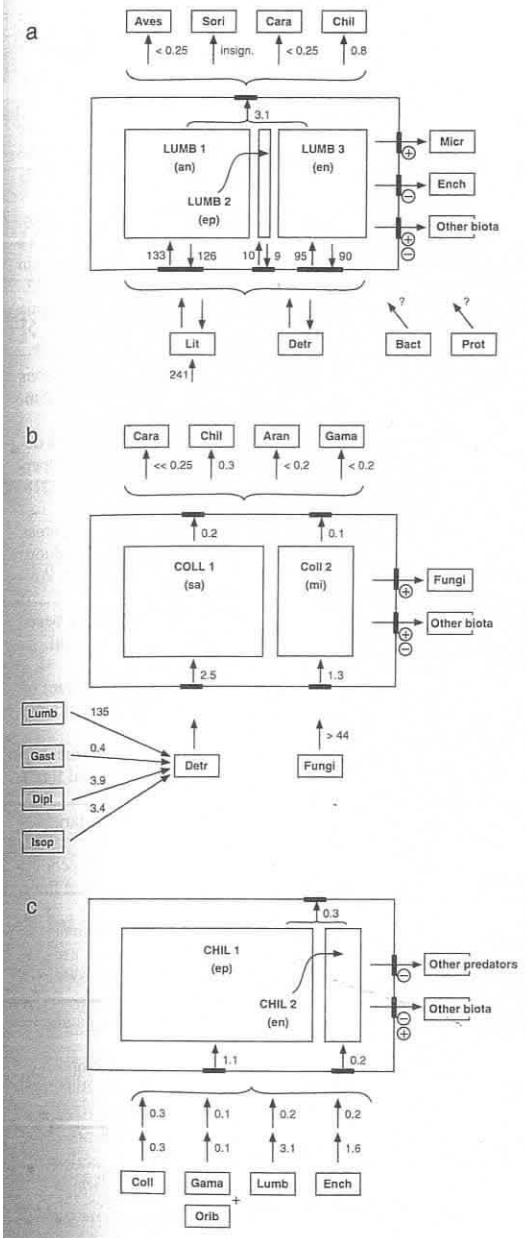

Fig 4. The interacting biotic system elements of Lumbricidae (a), Collembola (b), and Chilopoda (c) in a temperate forest with mull soil ("Göttinger Wald", Germany). Numbers denote rate of carbon flow as g C / m^2 / yr. Values were calculated from energy budgets in Schaefer (1990). + = direct or indirect positive effects, – = direct or indirect negative effects. an = anecic, ep = epigeic, en = endogeic. Micr = microflora. sa = saprophagous, mi = microphytophagous. Input rates (in c) at the interface "consumption" are based on direct estimates by Poser (1990) obtained with the ELISA technique. For further explanation see Fig. 2, Fig. 3 and text.

Chilopoda

Centipedes represent c. 2% of total zoomass in the studied forest. Epigeous litter-inhabiting species (Lithobiomorpha and *Strigamia acuminata*) dominate (84% of biomass) over endogeous forms (Geophilomorpha with 16% of the biomass) (Poser 1990). The centipedes feed on a variety of prey groups (Fig. 4c; cf. Fig. 3) and harvest a large proportion of prey production. Scarcity of prey and the presence of potentially competing predator groups suggest that centipedes in the forest tend to be food-limited.

Experiments demonstrated the high feeding pressure on collembolans and centipedes (as intra-guild predation) (Poser 1990). These results, too, support arguments that centipedes are food-limited.

5.3. Prospects for a synthesis

The final purpose is to fit all interacting biotic elements together on the basis of the trophic network presented in Fig. 3. Clarification of input-output relations and fluxes at the interfaces could help to understand the organisation of the system. Grazing pressures and modes of resource utilization could be quantified for whole trophic levels.

A tentative assessment of the validity of the proposed hypotheses given above is that the first set of hypotheses at least partly applies. In the saprophage pathway of carbon flux, the decomposers (lumbricids, enchytraeids, diplopods, isopods, gastropods) are food-limited and are only loosely connected to predatory groups. In the microflora pathway of carbon flux, the fungi and bacteria are limited by resource availability. Mesofaunal and microfaunal consumers of microflora are subject to high predation pressures which contribute to the limitation of population densities in both community elements. Continuing this line of reasoning, interspecific competition between constituent populations of the trophic elements must be prevalent in situations of overall resource limitation. However, further experimental evidence has to accumulate before a final answer can be given.

6. Conclusions

A bottom-up approach of building the system from its components, the interacting biotic elements, can contribute to understanding the organisation of the soil community. It should be emphasized, however, that the biotic network approach poses problems. In many cases it is difficult to delimit the interacting biotic systems. Their relation web may be oversimplified. Without paying attention to variations in the system, integration over time and space may obscure dynamic interactions at interfaces between elements. I have not included some features such as heterogeneity, patchiness, stochasticity, indirect facilitation, and organization in interactive hierarchies. When the many elements are assembled into a whole system, it may be difficult to detect causalities in the network of interrelations (Anderson 1987). In the extreme, all these difficulties and obstacles may mean

that it is impossible to study the soil community by the simple bottom-up assembly of biotic elements. If this is the case, a systems analysis precludes the inclusion of biotic diversity. A possible solution to this problem is the introduction of refined and sensitive field experiments as perturbations on an ecosystem level (e.g. increase of nutrient input for the microflora or the manipulation of leaf litter input) or experimental manipulation of population density in the field (e.g. exclusion of predators).

Acknowledgements. This paper benefitted from discussion with J. Schauermann, V. Wolters and M. Judas, Göttingen, and D.H. Wise, Baltimore. An anonymous referee gave helpful comments.

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